

# Changes in the Millipede (Diplopoda) Community during Secondary Succession from a Wheat Field to a Beechwood on Limestone

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## ABSTRACT

The diplopod communities of five sites, which were chosen to represent different stages of secondary succession from a wheat field to a beechwood on limestone (wheat field, 4 year old fallow, 11 year old fallow, ca 50 year old fallow, beechwood), were studied for 2 years. The sites were located in close proximity on a limestone plateau east of Göttingen (southern Lower Saxonia, Germany). Diplopods were extracted by heat from soil cores four times a year. A total of 12 species were found: *Allajulus nitidus*, *Cylindroiulus caeruleocinctus*, *Leptoiulus belgicus*, *Unciger foetidus*, *Tachypodoiulus niger*, *Ommatoiulus sabulosus*, *Blaniulus guttulatus*, *Mycogona germanicum*, *Glomeris marginata*, *Glomeris conspersa*, *Stygioglomeris crinita*, *Polydesmus inconstans*. Number of species, density and biomass increased up to the 11 year old fallow stage. They were considerably lower in the 50 year old fallow (ash dominated wood) and seemed to have increased again until the formation of the climax ecosystem of the beechwood. In contrast to succession theory, no continuous change in species composition occurred; rather, diplopods flourished at intermediate stages of secondary succession. Changes in community structure are discussed and related to environmental factors. Canonical correspondence analysis indicated the great importance of the amount of litter and of humidity for the species composition of diplopods. The most important determining factor for low diversity, density and biomass of millipedes at the 50 year old fallow is assumed to be the absence of a litter layer during summer.

## RÉSUMÉ

Variations dans un peuplement de diplopodes au cours d'une succession secondaire, d'un champ de blé à une hêtraie sur calcaire.

Les peuplements de diplopodes ont été étudiés pendant deux ans dans cinq sites voisins, représentatifs des différents stades d'une succession allant d'un champ de blé à une hêtraie sur calcaire (champ de blé, jachère de 4 ans, jachère de 11 ans, friche de 50 ans, forêt de hêtres). Les stations sont situées sur un plateau calcaire à l'est de Göttingen (Allemagne). Les diplopodes ont été obtenus par échantillonnage de carottes de sol et extraction sélective 4 fois par an. Douze espèces ont été récoltées : *Allajulus nitidus*, *Cylindroiulus caeruleocinctus*, *Leptoiulus belgicus*, *Unciger foetidus*, *Tachypodoiulus niger*, *Ommatoiulus sabulosus*, *Blaniulus guttulatus*, *Mycogona germanicum*, *Glomeris marginata*, *Glomeris conspersa*, *Stygioglomeris crinita*, *Polydesmus inconstans*. La richesse spécifique, la densité et la biomasse augmentent jusqu'au stade jachère de 11 ans. Elles sont nettement plus faibles dans la friche de 50 ans (Frêne dominant) et semblent de nouveau augmenter jusqu'à la formation forestière "climacique" de la hêtraie. A l'encontre de la théorie des successions, aucun changement continu n'apparaît dans la composition spécifique ; on observe plutôt un développement florissant du peuplement de diplopodes durant les stades intermédiaires de la succession. Les variations de cette structure sont discutées et mises en relation avec les facteurs environnementaux. Une analyse de correspondances canonique montre la grande importance de l'apport de litière et de l'humidité dans la composition spécifique des diplopodes. Le

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facteur déterminant les faibles diversité, densité et biomasse de diplopodes dans la friche de 50 ans semble être l'absence de litière durant l'été.

## INTRODUCTION

Diplopod communities of forest ecosystems (DUNGER, 1958; BLOWER, 1979; GEOFFROY, 1981; MEYER *et al.*, 1984; AXELSSON *et al.*, 1984) and arable fields (HERBKE, 1962; PETERS, 1984; KLINGER, 1992) have been frequently investigated. In addition, diplopods on restored mining soils found considerable attention (DUNGER, 1968; NEUMANN, 1971; DUNGER, & VOIGTLÄNDER, 1990). In contrast, little is known about changes in diplopod communities during secondary succession, e.g. after cessation of cultivation (TAJOVSKY, 1990).

Studies on secondary succession up to the climax are, for practical reasons, usually performed at different sites representing different stages of secondary succession. In the present study five sites were chosen to investigate changes in species composition, density and biomass of diplopods during secondary succession from an arable field to the climax ecosystem of a beechwood (*Fagus sylvatica* L.). The sites were located on a limestone plateau east of Göttingen (southern Lower Saxonia, Germany), most of them in close vicinity. The first site was an arable field which had been planted with wheat. The second and third sites had been left uncultivated for 4 and 11 years, respectively. The fourth site had been left abandoned for ca 50 years and a tree layer mainly of ash (*Fraxinus excelsior* L.) had grown up at this site. The fifth site was a beechwood which has been studied intensively (cf. SCHAEFER, 1991).

The present study forms part of a project which investigated changes in density and biomass of soil animals during secondary succession in combination with functional aspects of soil invertebrates for carbon turnover and nutrient cycling (SCHEU 1990a, b, 1992; SCHULZ, 1992; WOLTERS, in prep.). The aim of the present study was to get a closer understanding of the factors responsible for changes in the millipede community during secondary succession.

## MATERIALS AND METHODS

### *The sites*

Five sites representing different successional stages from a wheat field to a beechwood were investigated. The sites were located on a limestone plateau (360-420 m) east of Göttingen (Lower Saxonia, Germany). The wheat field was planted with wheat during the investigations. In general, a rotation of wheat, barley and rape has been planted on that field during the previous 20 years. Straw residues were burnt in autumn and the field worked with a disk cultivator. The second site (first fallow) had been left uncultivated for 4 years until 1987. The flora consisted of a mixture of weeds and grasses. The third site (second fallow) had been left uncultivated for 11 years and grasses dominated at this site. The floral composition indicated a decrease in nitrogen supply until this stage (cf. SCHEU 1990b). The fourth site (third fallow) had been left uncultivated for ca 50 years and was now an ash (*F. excelsior*) dominated wood. Ash trees had overgrown shrubs which were still present but in a stage of die back. The fifth site was a ca 130 year old beechwood (*F. sylvatica*) which has been described in more detail in SCHAEFER (1991). More details on the other sites can be found in SCHEU (1990a, 1992).

The climate in the study area is characterized by mild winters and humid summers. The annual mean temperature in Göttingen is 8.7°C and the annual mean precipitation 613 mm. Variation among years is considerable and there might be longer frost periods in winter and dry periods in summer; the former was the case in February 1987, whereas the latter occurred in May and to a lesser extent also in August 1988 (Fig. 1).

The soil water content varied during the year with a maximum in late winter and spring (Fig. 2). Variation was most pronounced in the litter layer and similar in the 0-3 and 3-6 cm soil depths. Generally, the water content of the soil was similar in the arable field and the fallow sites and considerably lower than in the beechwood.

The amount of carbon and nitrogen (determined by an elemental analyser; Carlo Erba, Milano, Italy) in 0-3 and in 3-6 cm soil depth was similar in the arable field and the two younger fallow sites and considerably lower than in the ash dominated wood and the beechwood (Fig. 3). The increase in the amounts of carbon and nitrogen in the two woodlands was caused by an accumulation of humus in the upper soil layers of these ecosystems which was accompanied by a decrease in soil bulk density. Mean annual amount of carbon and nitrogen in the litter layer was at a maximum in the fallow sites but varied considerably during the year. Litter material at the first fallow consisted mainly of weed residues, whereas grass leaf litter dominated at the second fallow. Litter materials estimated are presumably somewhat too high, particularly for the 4 year old fallow, because the above ground vegetation was partly included in material taken as litter.



In the ash wood most of the litter consisted of small twigs and branches from overgrown shrubs, the leaf litter had disappeared almost entirely by spring. In the beechwood a litter layer of beech leaves was present throughout the year.

#### Faunal investigations

Soil cores of 0.036 m<sup>2</sup> were taken from the study sites and separated into litter layer, 0-3 and 3-6 cm soil depth in the field. Eight randomly distributed samples were taken at 3 month intervals from October, 1986 to October, 1988 except for the third fallow which was investigated from October, 1987 to October, 1988 only. Diplopods were extracted by heat using a modified Kempson extractor (KEMPSON *et al.*, 1963, SCHAUERMANN, 1982) and determined to species level. The biomass was estimated using regressions between the body diameter and ash free dry mass established by SPRENGEL (1986) for *Mycogona germanicum* (Verhoeff, 1897) and *Allajulus nitidus* (Verhoeff, 1891). Biomass of *Cylindroiulus caeruleocinctus* (Wood, 1864), *Leptoiulus belgicus* (Latzel, 1844), *Unciger foetidus* (C. L. Koch, 1838), *Tachypodoiulus niger* (Leach, 1815), *Ommatoiulus sabulosus* (Linné, 1758), *Blaniulus guttulatus* (Fabricius, 1798) and *Polydesmus inconstans* Latzel, 1884 was estimated using the formula for *A. nitidus*. For *Glomeris marginata* (Villers, 1789) and *G. conspersa* (C. L. Koch, 1847) regressions between the width of the collum and ash free dry mass were used (SPRENGEL, 1986). The regression for *G. marginata* was also used to calculate the biomass of *Stygioglomeris crinita* Bröleman, 1913.

#### Statistical analysis

Canonical correspondence analysis (CCA, TER BRAAK, 1988) was used to ordinate samples and to relate diplopod data to environmental factors. Environmental factors (water content, carbon content, nitrogen content, C/N ratio, amount of carbon, amount of nitrogen) were determined from the litter material, 0-3 and 3-6 cm soil depth of small soil cores taken in close vicinity to the core for faunal extractions. Only four cores were taken at each sampling date at each site for determination of environmental factors and therefore, only diplopods from the adjacent four cores were ordinated. The water content in 3-6 cm soil depth was excluded from the analysis because of the collinearity with the water content in 0-3 cm (cf. Fig. 2). The amount and content of carbon and nitrogen in 0-3 and 3-6 cm soil depth was excluded because the correlation with species axes was poor ( $r < 0.3$ ). Eigenvalues obtained by CCA ordination were compared with those of DCA (detrended correspondence analysis; cf. TER BRAAK, 1988) ordination to estimate the relevance of the environmental factors included in the analysis.

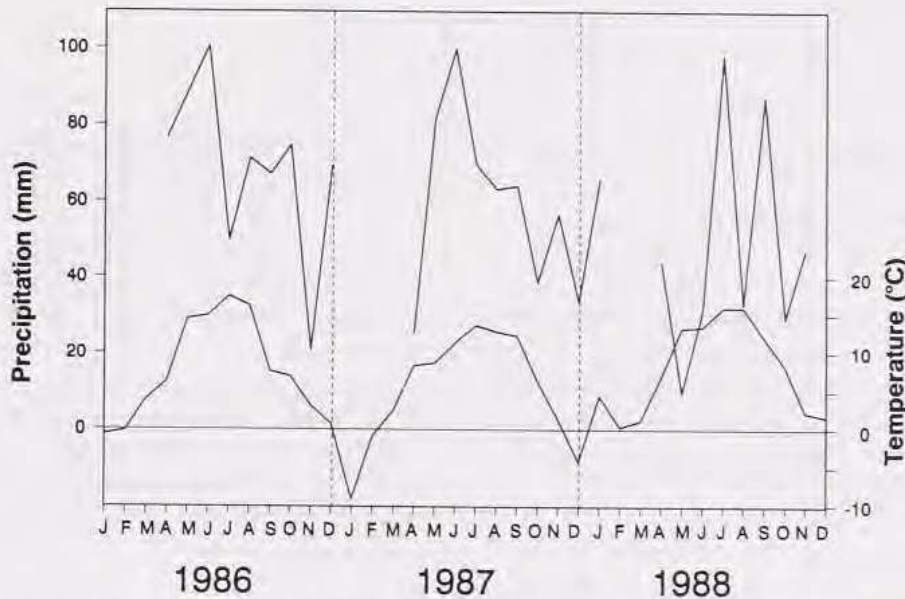


FIG. 1. — Monthly mean temperature and precipitation at the study sites in 1986-1988 (data were kindly provided by the Institute for Soil Science, Göttingen).

## RESULTS

### Species composition

A total of 12 diplopod species were found. Six species of Julidae (*A. nitidus*, *C. caeruleocinctus*, *L. belgicus*, *U. foetidus*, *T. niger*, *O. sabulosus*) and three Glomeridae (*G. marginata*, *G. conspersa*, *S. crinita*). The other three species belonged to three different



families: *B. guttulatus* (Blaniulidae), *M. germanicum* (Chordeumatidae), *P. inconstans* (Polydesmidae).

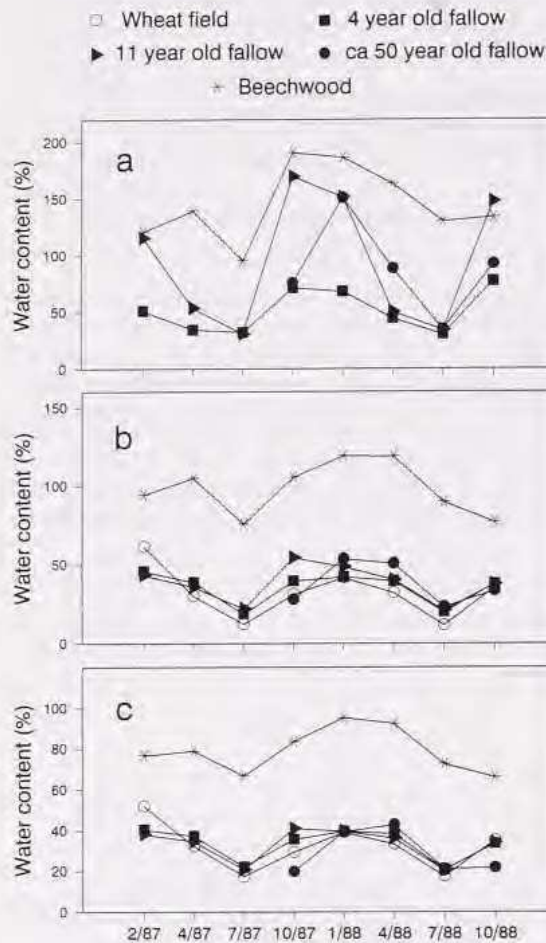


FIG. 2. — Changes in gravimetric soil water content in the litter layer (a), 0-3 (b) and 3-6 cm soil depth (c) at five sites representing different stages of secondary succession during 1987 and 1988.

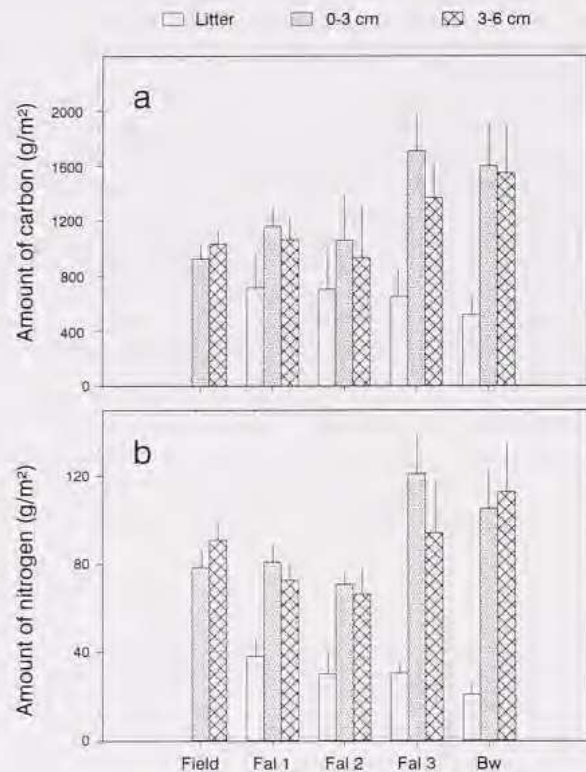


FIG. 3. — Amount of carbon (a) and nitrogen (b) in the litter layer, 0-3 and 3-6 cm soil depth of the study sites (means + SD of samples taken at 3 month intervals during 1987 and 1988; Field, wheat field; Fal 1, 4 year old fallow; Fal 2, 11 year old fallow; Fal 3, ca 50 year old fallow; Bw, Beechwood).

Species composition at the study sites was very different (Fig. 4). At the arable field five species were found. However, *A. nitidus* and *S. crinita* were found only once (adult females in both cases) and *C. caeruleocinctus*, in very small numbers (adult male, adult female and a specimen of stage 3). It is doubtful therefore, if these species formed autochthonous populations on the wheat field. Two species (*P. inconstans* and *B. guttulatus*) were found frequently and different stages were present.

At the 4 year old fallow a total of 10 species was found (Fig. 4). Except for *U. foetidus* juveniles were found, indicating that almost all of these species had reproduced on that site. At the 11 year old fallow 11 species were present. From each of these species juveniles were found



indicating that these species formed autochthonous populations. In comparison to the 4 year old fallow a considerably higher ratio of specimens older than 5 years was present at the 11 year old fallow, particularly for *A. nitidus* and *C. caeruleocinctus*. At the ca 50 year old fallow only five species were present. Only one specimen of *C. londinensis* in stage 6 was found and it remains unclear if this species was able to reproduce on this site. In the beechwood six species were present, adults and juveniles of each of them were found. Despite the similar number of species in the beechwood and the ca 50 year old fallow, the species composition was very different (Fig. 4).

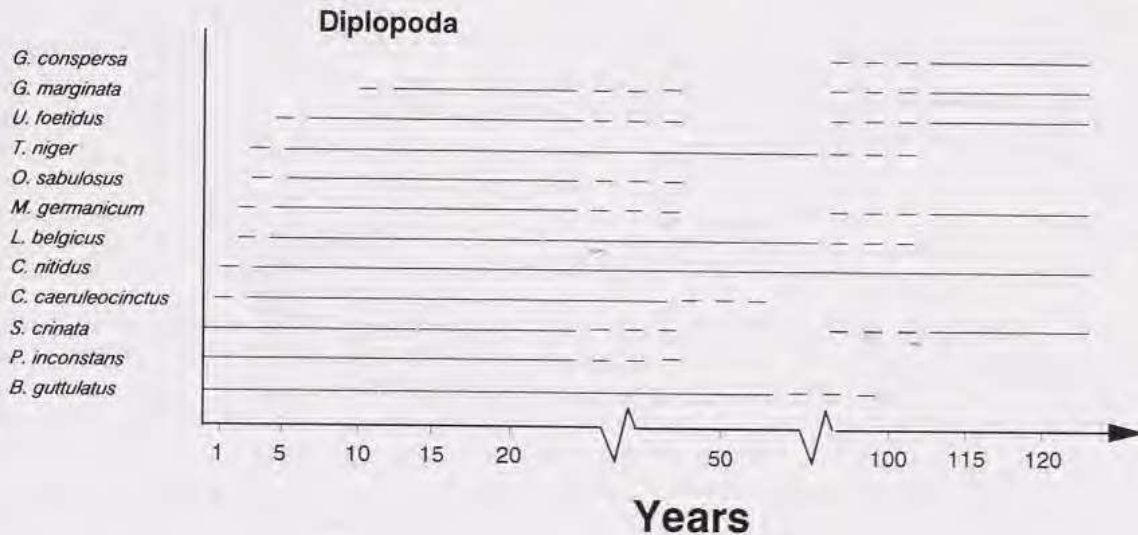


FIG. 4. — Changes in species composition of diplopods during secondary succession from a wheat field to a beechwood on limestone as indicated from the presence of diplopod species at five sites representing different stages of secondary succession.

### Density and biomass

Mean density and biomass of diplopods at the arable field were almost identical in 1987 and 1988 (Table 1). Of the two dominating species, *B. guttulatus* contributed more to mean annual density and biomass than *P. inconstans* (Fig. 5). Generally, density and biomass of millipedes were high in spring and autumn and few animals were found in winter and summer.

Density and particularly biomass of diplopods at the 4 year old fallow was considerably higher than at the arable field (Fig. 6). Biomass at the 4 year old fallow peaked in autumn and only few specimens were found in winter (Table 1). *A. nitidus* dominated in density and biomass (Fig. 5) indicating that this species was the most successful colonizer during early secondary succession. Two other julid species (*C. caeruleocinctus*, *L. belgicus*) also contributed significantly to density and biomass at this site.

At the 11 year old fallow density and biomass of diplopods were generally similar to that at the 4 year old fallow, however, mean annual density at the 4 year old fallow exceeded that at the 11 year old fallow in 1987 whereas mean annual biomass at the 11 year old fallow exceeded considerably that at the 4 year old fallow in 1988 (Table 1). Similar to the 4 year old fallow, *A. nitidus* dominated in density at the 11 year old fallow (Fig. 5). *A. nitidus* and *C. caeruleocinctus* also contributed significantly to biomass in the latter, but the larger julid species *O. sabulosus* dominated, despite its low numbers. As in the 4 year old fallow biomass of the millipedes usually increased during the year and peaked in autumn.



TABLE 1. — Changes in density and biomass of diplopods at five sites representing different stages of a secondary succession from October 1986 to October 1988. ND = not determined.

| Density (ind/m <sup>2</sup> )         |       |      |      |      |       |      |      |      |       | Mean |      |
|---------------------------------------|-------|------|------|------|-------|------|------|------|-------|------|------|
|                                       | 10/86 | 1/87 | 4/87 | 7/87 | 10/87 | 1/88 | 4/88 | 7/88 | 10/88 | 1987 | 1988 |
| Field                                 | 88    | 4    | 112  | 4    | 49    | 14   | 49   | 11   | 77    | 42   | 38   |
| First fallow                          | 95    | 46   | 98   | 137  | 343   | 32   | 126  | 70   | 179   | 156  | 102  |
| Second fallow                         | 270   | 63   | 84   | 95   | 165   | 70   | 130  | 53   | 182   | 102  | 109  |
| Third fallow                          | ND    | ND   | ND   | ND   | 242   | 0    | 28   | 18   | 81    | ND   | 32   |
| BeechWood                             | 147   | 46   | 63   | 49   | 116   | 28   | 39   | 77   | 88    | 68   | 58   |
| Biomass (mg dry mass/m <sup>2</sup> ) |       |      |      |      |       |      |      |      |       | Mean |      |
| Field                                 | 127   | 8    | 172  | 5    | 80    | 17   | 105  | 19   | 108   | 66   | 62   |
| First fallow                          | 1541  | 77   | 612  | 459  | 1455  | 93   | 976  | 320  | 1175  | 651  | 641  |
| Second fallow                         | 1102  | 450  | 606  | 294  | 744   | 1665 | 947  | 414  | 1956  | 524  | 1246 |
| Third fallow                          | ND    | ND   | ND   | ND   | 936   | 0    | 65   | 76   | 387   | ND   | 132  |
| BeechWood                             | 567   | 90   | 511  | 175  | 1560  | 109  | 108  | 557  | 434   | 584  | 302  |

Density and biomass of millipedes at the ca 50 year old fallow were exceptionally low and similar to the field (Fig. 6). *A. nitidus* dominated in density and biomass. *L. belgicus* and *B. guttulatus* had a similar density but *L. belgicus* contributed more to biomass.

In the beechwood the density and biomass of millipedes seems to have increased considerably in comparison to the preceeding successional stage of the ca 50 year old fallow (Fig. 6). However, in comparison to the two other fallow sites density and biomass of diplopods were considerably lower in the beechwood. In the 4, 11 and ca 50 year old fallow sites *A. nitidus* dominated in density and biomass as in the beechwood, but two other species, *M. germanicum* and *G. marginata*, which were absent or rare at preceeding successional stages contributed significantly to diplopod density and biomass in the beechwood.

#### Species environment correlation

The biplot of diplopod species composition and environmental variables (Fig. 7a) showed a gradient from species which dominated in the wheat field (*P. inconstans*, *B. guttulatus*) to species which occurred mainly in the beechwood (*G. marginata*, *G. conspersa*, *U. foetidus*, *M. germanicum*). Species which were most abundant at the two younger fallow sites (*C. caeruleocinctus*, *O. sabulosus*) were separated from those which dominated in the beechwood by a moisture gradient and by a gradient in the amount of litter. As shown in Figure 3, the two fallow sites had the highest amounts of litter, whereas the beechwood was the most humid site (Fig. 2). The small difference in CCA eigenvalues (first axis 0.58, second axis 0.35) and DCA eigenvalues (first axis 0.74, second axis 0.46) indicate that a substantial part of the variation in species composition is represented by the environmental variables.

The CCA joint plot of samples showed four clusters (Fig. 7b). Parallel to the positions of *B. guttulatus* and *P. inconstans* (Fig. 7a), the dominating species at the wheat field, samples taken at this site were on the far right side of the diagram (first cluster). Positions of samples from the beechwood (second cluster) and the 4 and 11 year old fallow (third cluster) corresponded to the positions of the dominating species at these sites. Positions of samples from the third fallow (fourth cluster) indicate that there was no continuous change in environmental conditions during secondary succession in respect to the diplopod community. Environmental factors representing much of the diplopod variation at this site were similar to those at the arable field. Hence, in respect to the diplopod community, the arable field was most similar to the third fallow, contrasting the floral dissimilarity of the two sites.



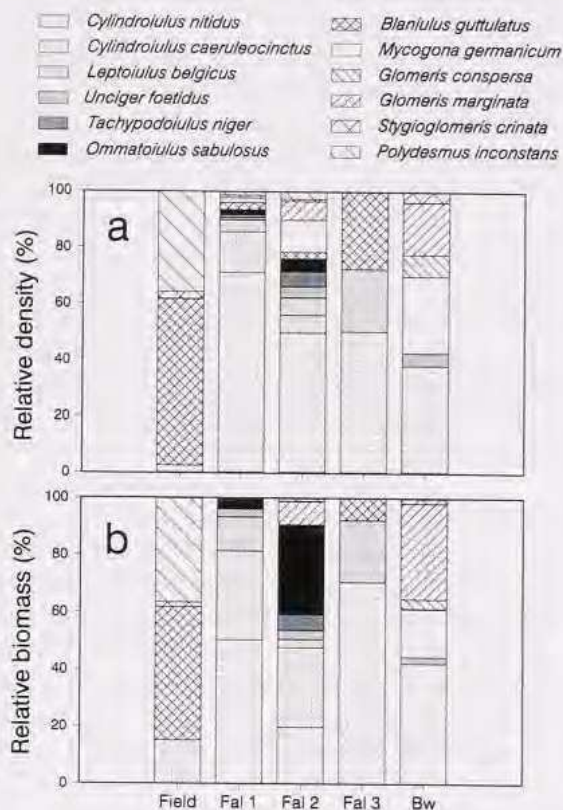


FIG. 5. — Dominance structure in density (a) and biomass (b) of diplopods at five sites representing different stages of secondary succession (legend see Fig. 3).

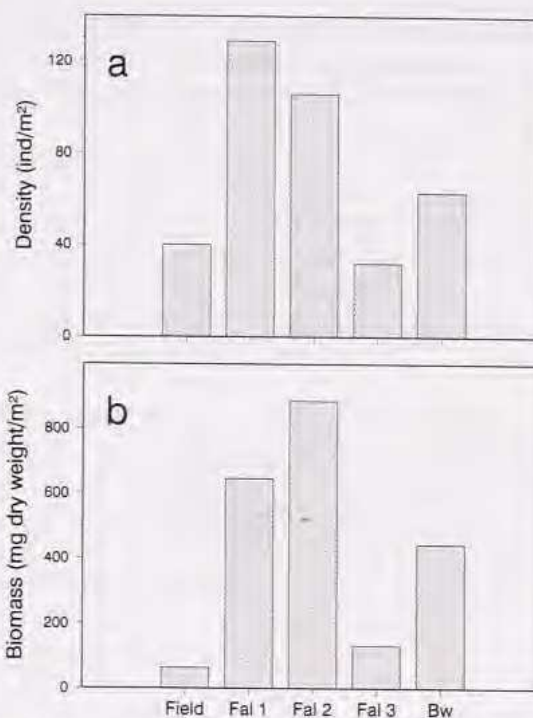


FIG. 6. — Density (a) and biomass (b) of diplopods at five sites representing different stages of secondary succession (means of 1987 and 1988 except for the third fallow which was investigated in 1988 only; legend see Fig. 3).

### DISCUSSION

Succession refers to a continuous change in species composition, with time, following a perturbation. To explain the changes in species composition three hypotheses were presented (CONNELL & SLATYER, 1977): facilitation, tolerance and inhibition. The facilitation hypothesis assumes that species of early successional stages improve environmental conditions for following species (ODUM, 1969). The tolerance model assumes that species of later successional stages are more specialized; the changes in species composition being independent of the preceding species. The inhibition model assumes that species which have colonized a distinct successional stage inhibit colonization by other species until their death. Most of these theories were developed in studies on plant communities or sessile marine animals, little attention has been paid to terrestrial animal communities.

The floral composition of the five sites investigated in the present study indicates a continuous change in plant species composition during secondary succession from the arable field to the beechwood (SCHEU, 1990b). In contrast to plants, the diplopod communities at the five sites indicate that no continuous change in millipede species occurs when arable fields are left uncultivated until formation of the climax ecosystem of a beechwood. Instead, diplopod species flourished at the 11 year old fallow and several species which occurred at this site were absent at the ca 50 year old fallow (*S. crinata*, *M. germanicum*, *U. foetidus*, *G. marginata*) but occurred again in the beechwood. Hence, the data indicate that several diplopod species become



extinct during secondary succession in an ash dominated stage and occur again in the climax ecosystem of the beechwood. TAJOVSKY (1990) also found diplopods to thrive in early stages of secondary succession. For a better understanding of changes in the diplopod community during secondary succession gradients in environmental factors should be considered.

The most extreme habitat for millipedes was the field. Cultivation presumably caused an extreme disturbance of the habitat and straw burning reduced the available food substrate. As a consequence, only species with a short life cycle (e.g. *P. inconstans*) or with a high reproductive

potential (r-strategists; e.g. *P. inconstans*, *B. guttulatus*) occurred at this site. Cessation of cultivation enabled a variety of diplopod species to colonize the abandoned fields. At the 4 year old fallow at least nine species formed autochthonous populations; at the 11 year old fallow 11 reproducing species were present.

One of the most important factors responsible for the thriving of diplopods at the 4 and 11 year old fallow sites was presumably the presence of a litter layer throughout the year. Litter material may have served as food substrate, but the presence of a litter layer might have also buffered temperature and moisture extremes, e.g. frost during winter and drought in summer. As indicated by CCA ordination, the occurrence of species typical of the 4 and 11 year old fallow (e.g. *C. caeruleocinctus*, *O. sabulosus*) was related to high amounts of litter at these sites. A second factor which might have been important in structuring the diplopod communities at these sites was humidity. CCA showed that the occurrence of millipede species typical of the 4 and 11 year old fallow was related to low moisture levels in litter and soil. Obviously, these species tolerate the low moisture levels which occur at these sites particularly during summer. *C. caeruleocinctus*, *O. sabulosus* and *T. niger* as well were considered to prefer warm dry habitats (e.g. HAACKER, 1968; THIELE, 1968; DUNGER & STEINMETZGER, 1981) indicating their tolerance for low humidity. Generally, the species composition and dominance structure of the diplopod community at the 11 year old fallow was similar to that of other fallow sites investigated

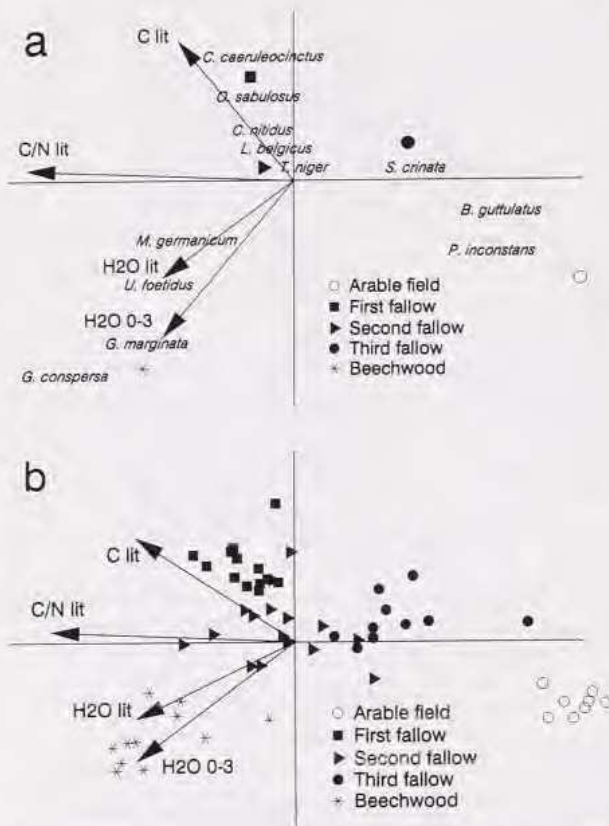


FIG. 7. — Canonical correspondence analysis biplot with environmental variables [amount of carbon in the litter layer (C lit), C/N ratio of the litter (CN lit) and gravimetric water content in the litter layer (H2O lit) and in 0-3 cm soil depth (H2O 0-3)] represented by arrows; (a) ordination of the composition of the diplopod community from five sites representing different stages of secondary succession with centroids of the five sites; (b) ordination of samples taken at the five sites (data from 1988; for details see text).

by STRÜWE-KUSENBERG (1981). In comparison to sites of similar age, which had been restored or developed on raw soils by primary succession (DUNGER, 1968; NEUMANN, 1971), the diplopod community at the 11 year old fallow resembled those of restored afforested sites.

In comparison with the younger fallow sites, and the beechwood, the ash dominated wood (ca 50 year old fallow) was an extreme habitat for millipedes. Only few species were present and the density and biomass was low, resembling that of the wheat field. Low diversity, density and



biomass of diplopods in the ash dominated wood was unexpected because it has been shown frequently that ash leaf litter is a preferred food substrate by diplopods (DUNGER, 1958, 1962; SAKWA, 1974). However, ash leaves are also known to decompose quickly. Ash leaf litter in the ca 50 year old fallow had already disappeared almost entirely by May. The litter layer during summer, until shedding of leaves in autumn, consisted mainly of small branches and twigs from the overgrown shrub layer. The woody materials were presumably of low nutritional value for diplopods and did not form a litter layer suitable for buffering extremes in temperature and moisture.

The beechwood was characterized by the absence of species typical of the open fallow sites and the arable field and by the occurrence of *G. conspersa*. In addition, *G. marginata* and *M. germanicum* were most abundant at this site. CCA indicated that the occurrence of these species was related to humid conditions. It has been frequently found that these species preferentially colonize wooded habitats, especially *G. conspersa* which is known to occur almost exclusively in moist woodlands (BEYER, 1964; THIELE, 1968; BROCKSIEPER, 1976). The colonization of more humid ecosystems by these species presumably is related to a low tolerance of dry conditions during summer.

The content of organic matter in the upper soil layers at the five study sites indicate that wood formation was accompanied by a strong increase in soil humus. It was hypothesized by SCHEU (1992) that this increase is of considerable importance for the changes in the lumbricid community during secondary succession. In contrast, results of the CCA in the present study indicate that the soil humus content is of minor importance in determining the structure of diplopod communities. Rather, the analysis emphasized the importance of the litter layer.

The biomass of diplopods in the beechwood during the investigated period of 1987 and 1988 averaged 443 mg dry mass/m<sup>2</sup>. Variation between years in density [coefficient of variation (CV) = 11%] was considerably lower than that in biomass (CV = 45%). The biomass at the 11 year old fallow also varied considerably between 1987 and 1988 (CV = 58%), whereas the density was almost identical (CV = 1%). There was no unidirectional change in density or biomass of the diplopod communities at the study sites from 1987 to 1988. The mean annual biomass of diplopods at the 4 year old fallow and the wheat field remained at a very constant level. At the 11 year old fallow it increased considerably (+138%), whereas in the beechwood it decreased strongly (-48%). The summer in 1988 was exceptionally dry, particularly in May, but also in August (Fig. 1). Biomass data suggest that these unusually dry conditions did not have detrimental effects on the diplopod communities of the younger fallow sites and the arable field but did on that of the beechwood (density at the 4 year old fallow might also have been affected). Presumably, the diplopod community of the beechwood is more susceptible to drought, despite the buffering capacity of the canopy of trees and the presence of a litter layer throughout the year. In a six year investigation SPRENGEL (1986) also concluded that dry summers adversely affected density and biomass of millipedes at the beechwood, particularly in autumn.

In comparison to other woodlands, the density and biomass of diplopods at the beechwood was in an approximately central position (DUNGER, 1958; BLOWER, 1979; GEOFFROY, 1981; MEYER *et al.*, 1984; AXELSSON *et al.*, 1984). Diplopods are considered to be important agents for litter processing and nutrient cycling in forest ecosystems. The considerably higher biomass of diplopods at the younger fallow sites indicate however, that the effect of diplopods in these ecosystems may even exceed their effect in woodlands.

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